



Odonata community structure and patterns of land use in the Atewa Range Forest Reserve, Eastern Region (Ghana)

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Recent studies have indicated that frequent anthropogenic disturbances in tropical developing countries are primary drivers of reduction in community diversity and local extinction of many arthropods, including dragonflies. We assessed the impact of anthropogenic disturbances on odonate assemblages across three different land use types, in a biodiverse nature reserve in Ghana. A total of 37 transects (100 \times 10 m) were used to survey odonate species over two seasons and three rivers which pass through agricultural, mature forest and forest margin habitats. A total of 6940 individuals, belonging to 53 species (23 Zygoptera and 30 Anisoptera) in eight families, were recorded. Sapho ciliata (15% relative abundance) was the most abundant zygopteran, whereas Orthetrum julia (4.8% relative abundance) was the dominant anisopteran. Rarer species like Umma cincta, Chlorocnemis sp. and Elattoneura sp. were represented by < 50 individuals. The effective number of species was affected by the surrounding terrestrial habitat type and this most strongly reflected the difference between agricultural habitats (8.09 \pm standard error (SE) 0.41) and mature forests (5.0 \pm SE 0.24). A canonical correspondence analysis revealed that turbidity, surface water temperature, canopy cover and channel width were the key factors that influenced odonate assemblages. Degraded habitats were dominated by generalist and heliophilic dragonflies, while mature forest habitat included more stenotopic damselflies and dragonflies. These findings improve our understanding of the drivers of Odonata distributions and diversity and will help river managers use odonates to monitor riverine health, as part of conservation activities.

Keywords: dragonfly; fragmentation; generalist; specialist; heliophilic; agricultural habitat; mature forest; forest margin; effective number of species; canonical correspondence analysis; ecosystem health

Introduction

Humans are increasingly modifying natural habitats via fragmentation and conversion to agricultural, industrial, or urban habitats. Such land use changes are often linked to changes and declines in local biodiversity (Stuart et al., 2004; Todd & Rothermel, 2006). Increased demand for agricultural lands and other intensive land use matrices is a major driver escalating natural habitat loss and modification worldwide (Faruk, Belabut, Ahmad, Knell, & Garner, 2013; Henderson, 1997). Freshwater habitats, which support a significant component of global biodiversity, are increasingly threatened by anthropogenic impacts such as riparian deforestation, water abstraction for irrigation, fishing and industrial activities (Vörösmarty et al., 2010). Freshwater habitats

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contain 10% of all known species, in an area of only 1% of the Earth's surface (Strayer & Dudgeon, 2010), and provide ecosystem services valued at several trillion USD per year globally (Postel & Carpenter, 1997). More than half of Earth's wetlands have been degraded under intensified land use practices (Russi et al., 2013), and more than two-thirds of upland watersheds are not protected (Thieme et al., 2010). Overall, freshwater ecosystems and freshwater biodiversity are under great peril, and urgent measures are needed to protect remaining natural freshwater habitats (Garcia-Moreno et al., 2014).

Furthermore, recent studies have indicated that frequent anthropogenic disturbances in tropical developing countries are primary drivers of reduction in community diversity and local extinction of many arthropods (Clausnitzer et al., 2009; Lawton et al., 1998). For example, oil-palm plantations are associated with reduced species richness, species diversity and shifts in community composition in beetles (Chung, Eggleton, Speight, Hammond, & Chey, 2000) and ants (Brühl & Eltz, 2010). Studies on dragonflies have documented similar declines under intensified land use in tropical (Clausnitzer, 2003; Samways, 2003) and subtropical (Stewart & Samways, 1998) regions. Intensified land use has also been shown to result in changes in species composition. Specifically, specialists tend to be replaced by more widespread generalists following habitat disturbances caused by human activities (see Koch, Wagner, & Sahlén, 2014).

Understanding the changes in African biodiversity in response to human activities requires the study of species that respond readily to environmental stress. Insects represent just such a key indicator group, because they are known to quickly respond to environmental stressors and modified ecosystems (Koch et al., 2014). The insect order Odonata comprises damselflies (suborder Zygoptera) and dragonflies (suborder Anisoptera), and includes species that are variously sensitive to anthropogenic influences such as farming and forestry (Koch et al., 2014). Odonates have received increasing attention worldwide from conservationists and ecologists as critical indicators of habitat degradation and ecosystem change. Odonates are widely used as indicators of the health of the freshwater habitats and the environment (Ameilia, Che Salmah, & Hassan, 2006; Clausnitzer, 2003), because of their sensitivity to alteration habitat structure (e.g. Clark & Samways, 1996; Dijkstra, 2007; Samways & Steytler, 1996; Stewart & Samways, 1998; Steytler & Samways, 1995).

In Ghana, studies on the impact of ecosystem disturbance on biodiversity have primarily focused on amphibians (Ofori-Boateng et al., 2013), butterflies (Addo-Fordjour, Osei, & Kpontsu, 2015), and other terrestrial arthropods (Belshaw & Bolton, 1993). Studies on odonate responses to ecosystem disturbance in Ghana are scant, despite the fact that odonatological studies in Ghana date back as far as 1871 (Dijkstra, 2007), with 177 species recorded to date (D'Andrea & Carfì, 1994; Dijkstra, 2007; Frempong & Nijjhar, 1973; Marshall & Gambles, 1977; Neville, 1960; O'Neill & Paulson, 2001; Pinhey, 1962).

The Atewa Range Forest Reserve in Ghana, which is the focus area for this study, is designated as a globally significant biodiversity area and is home to many endemic and threatened species of wildlife including birds, butterflies, black star plants, and odonates (Abu-Juam et al., 2003; Dijkstra, 2007; Hawthorne 1998; Larsen, 2006). The Atewa Range Forest Reserve also includes the headwaters for many major river systems in Ghana, namely the Sumatua, Suhen, Kuia, Ayensu, Birim, Adensu, Supon and the Densu river basins, of which the latter supplies one third of the water required for domestic, industrial and agriculture irrigation by the people of Greater Accra region (Acquah-Lamptey, Kyerematen, & Owusu, 2013). These water bodies are the main source of drinking water to the fringe communities as well. Thus, understanding the impacts that human activities have on the freshwater resources within the reserve is important for both biodiversity conservation and human welfare.

The reserve is under intense pressure from agriculture, illegal logging and small scale mining activities, which threaten both terrestrial and freshwater habitats and the diverse species therein. Prior to this study, it was unknown how deforestation and other disturbances impact

the freshwater habitats and the odonate assemblages in this region. However, understanding the species responses to disturbance dynamics will help prioritize the best management practices for sustaining habitat quality, biodiversity, and ecosystem services within the reserve. The aim of this study is to determine the impact of different land use patterns on Odonata community structure, and to explore the potential of using changes in these communities as an assessment tool in monitoring freshwater habitat degradation, in order to prioritize conservation intervention.

Materials and methods

Study area

The study was conducted along three rivers (the Densu, Adensu and Supon Rivers) in the Atewa Range Forest Reserve (ARFR) in the Eastern region of Ghana (Figure 1). These three rivers each pass through different land use matrices, which make them ideal for comparing Odonata assemblages along gradients of land use intensity. The rivers lie at 5°58′-6°20′ N, 0°31′-0°41′ W in the ARFR. The natural forest vegetation alongside all of these rivers is adversely impacted by widespread agricultural activities, such as cocoa and vegetable farming. The forest margin habitat along all three rivers is characterized by secondary forest (forests regenerating largely through natural processes after significant removal or disturbance of the original forest vegetation by human or natural causes) where farming, small scale mining and logging activities are intensive. Densu River is located in the Protroase area of the ARFR, as is at lower elevation than the Adensu and Supon rivers. Thus its natural forest habitat has been more strongly impacted by human activities, with only few trees left on the river banks constituting gallery forest (a narrow strip of forest along the banks of the watercourse). In contrast, the Adensu and Supon

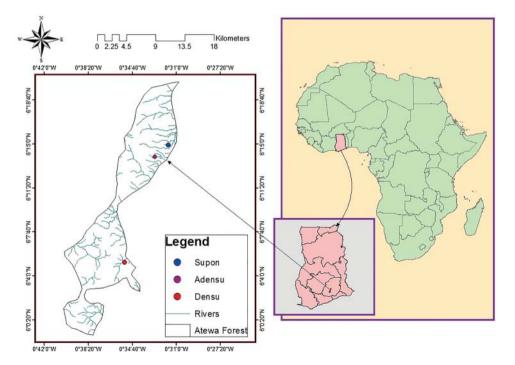


Figure 1. Map of the Atewa Range Forest Reserve showing the various rivers sampled.

rivers, which are located in the more mountainous Sagyimase area of the ARFR, are surrounded by more intact natural forest habitats, particularly towards higher-elevation sites where agriculture, logging, and mining are less effective. The surrounding forest margins through which these rivers subsequently pass, however, are subjected to widespread small-scale mining operations, deforestation, and agricultural activities which are similar to land use activities along the Densu. These land use activities have contributed to degrading the water quality, including increased turbidity and pollution, in all three rivers. Annual precipitation in the study region is between 1200 mm and 1800mm, and the average temperature is 27°C (Abu-Juam et al., 2003). The soil types are primarily lithosols, red clays and ochrosols from the Birimean rock formation (Hall & Swaine, 1976). About 75% of the reserve is topographically complex (Hall & Swaine, 1976), with elevations ranges of 200–750 m. The native vegetation in the study area is typical of moist semi-deciduous forests in Ghana and contains endemic species such as *Medinilla enti*, *Anthocleisia obanensis*, *Aframomum atewa* and *Piper capense* (Hawthorne & Abu-Juam, 1995).

Sampling procedure

Sampling of adult odonate species was carried out across different land use types on each of the three rivers, namely: agricultural (open banks with cocoa and vegetable farming), mature forest (intact natural forest) and forest margin (secondary forest) habitats. A belt transect of 100 m × 10 m, with a sampling effort of 2 fieldworkers \times 40 min was used to sample the adult odonates. A total of 37 transects and 148 sampling events (four sampling visits per transect) were used to survey the species. Eleven transects were located in the agricultural habitat (nine on Densu River and two on Adensu River), 14 transects were located in the mature forest (five on Densu River, four on Supon River and five on Adensu River) and 12 transects in the forest margin (six on Densu River, and three transects each laid on the Adensu and Supon rivers). The forest margin transects were chosen at least 100 m from the borderline of the mature forest along the rivers. All transects for forest margin habitat were chosen within allocated areas specially demarcated by the Forest Service Division of the Forestry Commission as forest margin. The mature forest habitat transects were chosen 100 m from the boundary lines into the interiors of the pristine forest habitats, while agricultural habitat transects were equally chosen at least 100 m away from the forest margin. Owing to seasonality of adult recruitment (Corbet, 1999), each transect was visited twice in each season (wet and dry season) to capture a representative spectrum of species diversity (Schmidt, 1985). The wet season sampling was done in June 2015 and October 2015 whilst the dry season sampling took place in December 2015 and January 2016. The sampling was done during the day between the hours of 10 am and 4 pm. A hand net was used to capture all adult odonate species present (i.e. either flying or perching) when possible and identified in situ, using keys developed by Dijkstra and Clausnitzer (2014). Species were further classified as generalists (widespread in most open habitats and can also utilize forest habitats), specialists (forest species with narrower range of habitat tolerances) and heliophillics (species mostly found in open habitats and stagnant water bodies), using the Dijkstra and Clausnitzer (2014) guide and African Dragonflies and Damselflies Online (http://addo.adu.org.za). For species not in Dijkstra and Clausnitzer (2014), which is for Eastern Africa, we contacted Clausnitzer and Dijkstra for further assistance in providing species identifications.

Assessment of environmental variables

During sampling, abiotic variables were also recorded, to assess their influence on the odonate community structure. Surface water temperature (°C), dissolved oxygen (mg l⁻¹), conductivity (mS cm⁻¹), turbidity (Nsl), total dissolved solids (TDS) and pH were recorded with a U-50

Horiba water quality meter (HORIBA Instruments Incorporated Process and Environmental, Pasadena, TX, USA). These variables were recorded in both the wet and dry season.

The altitude, canopy cover, flow rate, river width and depth, aquatic and bankside vegetation, and presence of lagges (riverside pools created by small scale mining activities, which can provide alternative habitats for riparian odonates) were also recorded. For each transect, a measuring tape was used to assess mean river width by combining measurements of the river width three times at the beginning, midpoint and the end of the transect. The mean depth was assessed by submerging a pole in the water and the reading taking using tape measure at three points across the river for each transect. A Garmin GPS (etrex 10; Garmin Ltd, Canton of Schaffhausen, Switzerland) was used to take coordinates and altitudes of each transect. The canopy cover was assessed using a densiometer. The plant species at each transect were recorded as aquatic vegetation (plants in stream channel, partly or fully submerged), marginal or bankside vegetation (grass, shrubs, ferns, weeds, trees, etc.), and algae (free-floating or on stones), according to the classification of Gerber and Gabriel (2002). The presence of lagges and type of land use were also recorded.

Data analysis

Species relative abundance in the study area was obtained first by combining all of the wet and dry season records of each sampling transect, to explain variation in odonate assemblages according to the three land use types (agricultural, mature forest and forest margin habitats) across the three rivers, using the formula below:

Relative abundance =
$$\frac{\textit{Total number of individuals of an odonate species}}{\textit{Total number of individuals of all odonate species sampled}} \times 100\%$$
 (1)

The mean effective number of species (ENS) and mean species richness of odonates in the three habitats were estimated using jackknifing (Abdi & William, 2010), in the vegan package (Oksanen et al., 2016) for R (R Core Team, 2016). Jackknifing produces an unbiased parametric estimator of the variance of a sample mean, where observations are independent of each other (Abdi & William, 2010). ENS represents the inverse log of the Shannon-Weaver index of alpha (within-site) species diversity, and this transformation results in an alpha diversity measure that is represented in units comparable to raw species richness (numbers of species). Calculated values of ENS and species richness were treated as surrogates for local biodiversity (Marshall, Steward, & Harch, 2006). The pairwise Sørensen index (Sørensen, 1948) of dissimilarity was chosen to quantify beta diversity (composition dissimilarity) between habitat types. This index was chosen over the Jaccard coefficient, because it gives weight to the species that are common to both habitat types, rather than to those which are unique to either habitat (Kent, 2011). The Sørensen dissimilarity index model is as follows, where b represents the species unique to site 1, c represents the species unique to site 2, and a represents the species shared between two sites:

$$D_s = -\frac{b+c}{2a+b+c} \tag{2}$$

We first tested the data for conformity to a normal distribution using Shapiro-Wilks normality test. We determined the effects of habitat variables on species diversity (estimated as ENS and species richness), using a linear mixed-effects model (LMM) with a Gaussian error distribution (Schaalje, McBride, & Fellingham, 2002). In these models, random effect terms were included for river, visit, and sampling site (transect) within the river, to account for multiple samples taken at each site, and to account for site-specific effects unrelated to our measured variables (Ofori-Boateng et al., 2013). We also included the latitude and longitude of each transect site to account for the spatial variation among the various habitat types and the transects. LMMs were implemented in the lme4 and lmerTest packages for **R** (Bates, Martin, Bolker, & Walker, 2015; Kuznetsova, Per Bruun, & Rune, 2016). Alternative models were run by adding and substituting the fixed effect variables, and the best model was selected by choosing the model with the smallest possible Akaike's information criterion (AIC) (Gregoire & Schabenberger, 1996; Gutzwiller & Riffell, 2007). A canonical correspondence analysis (CCA) (Ter Braak, 1986) was also performed to determine the influence of environmental drivers of change on odonate diversity, abundance and spatial distributions, using the vegan 'envfit' function in **R**. A Monte Carlo test with 999 iterations was used to test for the significance of the eigenvalues generated by the first two axes in the analysis of the odonate community structure to habitat variables. All environmental predictor variables were tested for spatial autocorrelation (only non-correlated values were included together in models), and overdispersion of environmental values was ruled out using negative binomial regression (Poisson regression).

Results

Abundance, relative abundance and dominance of odonates

A total of 6940 individuals belonging to 53 species in eight families were sampled along the agricultural, mature forest and forest margin habitats in the Densu, Supon and Adensu rivers (Tables 1 and 2). Of the 53 recorded species in the study area, 23 belong to the suborder Zygoptera (damselflies) and 30 to the suborder Anisoptera (dragonflies). The abundance of each species along each of these three rivers and habitat types is provided as supplementary data (Appendices 3–5).

The most abundant species from the suborder Zygoptera was *Sapho ciliata*, with an estimated 15% relative abundance across all sites, followed by *Pseudagrion melanicterum* (11.2%) and *Chlorocypha luminosa* (10.8%). Rarer species such as *Umma cincta*, *Chlorocnemis* sp., *Lestes dissimulans*, *Elattoneura* sp. and *Chlorocypha curta* were detected at < 50 individuals each. The most abundant Anisoptera species was *Orthetrum julia*, which constituted 4.8% of the relative abundance, followed by *Trithemis arteriosa* (4.7%), *Palpopleura lucia* (4.3%), and *Palpopleura portia* (3.3%). *Gynacantha bullata* (a forest specialist species) from the Aeshnidae family was recorded only once in the study area, but this record is unlikely to represent the true frequency of this species, since they were active at dusk, outside of our regular sampling times.

Comparison of odonate species assemblages among agricultural, mature forest and forest margin habitats in the three rivers

The highest mean effective number of species (ENS) was calculated in the agricultural habitats (8.089 \pm standard error (SE) 0.410, n=44), followed by forest margin (6.750 \pm 0.276, n=48) and the mature forest habitat (4.998 \pm 0.238, n=56) (Figure 2). The mean species richness also followed a similar trend, with agricultural habitats exhibiting the highest total number of species per transect (10.227 \pm 0.545, n=44), followed by forest margin (8.479 \pm 0.364, n=48) and the mature forest (6.393 \pm 0.309, n=56) (Figure 3). The linear mixed effect model (LMM) indicated a significant effect of habitat type on ENS at an alpha-level significance threshold of 0.05, and this reflected differences in ENS of odonates between the mature forest habitat and the agricultural habitat (estimate (est) = 1.692 \pm SE 0.692, t = 2.445, p=0.021). Conversely, there was no significant difference in the ENS of odonates between the mature forest and the forest margin (est = 0.816 \pm 0.606, t = 1.346, p=0.188) or between the forest margin

Table 1. A complete list of the Zygopterans (damselflies) in the three habitat classes within the study area. Species classified as forest specialist are represented by asterisk (*), generalist species are represented by exclamation mark (!) and heliophilic species are represented by number sign (#), following Dijkstra and Clausnitzer (2014) and African Dragonflies and Damselflies Online (http://addo.adu.org.za)

Family	Zygoptera species	Agricultural habitat	Mature forest	Forest margin	Total	Relative abundance
Calopterygidae	Phaon camerunensis Sjöstedt, 1900*	18	99	45	162	2.33
1 70	Phaon iridipennis (Burmeister, 1839) *	19	46	35	100	1.44
	Sapho ciliata (Fabricius, 1781) *	230	542	268	1040	14.99
	Umma cincta (Hagen in Selys, 1853) *	0	46	1	47	0.68
	Chlorocypha curta (Hagen in Selys, 1853)!	32	0	17	49	0.71
	Chlorocypha luminosa (Karsch, 1893) *	194	311	249	754	10.86
	Chlorocypha radix Longfild, 1959!	46	8	8	62	0.89
	Chlorocypha selysi Karsch, 1899*	40	227	9	276	3.98
Lestidae	Lestes dissimulans Fraser, 1955*	0	3	0	3	0.04
Coenagrionidae	Ceriagrion glabrum (Burmeister, 1839) #	0	9	9	0.13	
-	Ceriagrion sp#	0	0	8	8	0.12
	Pseudagrion glaucoideum Schmidt, 1936!	0	0	6	6	0.09
	Pseudagrion hamoni Fraser, 1955#	137	33	28	198	2.85
	Pseudagrion kersteni (Gerstäcker, 1869)!	72	111	56	239	3.44
	Psuedagrion sp1	5	5	0	10	0.14
	Pseudagrion sp2	0	0	8	8	0.12
	Pseudagrion sjoestedti Förster, 1906*	2	2	10	14	0.20
	Pseudagrion melanicterum Selys, 1876!	266	180	329	775	11.17
	Pseudagrion epiphonematicum Karsch, 1891	21	0	4	25	0.36
Platycnemidae	Mesocnemis singularis Karsch, 1891!	396	0	0	396	5.71
Protoneuridae	Chlorocnemis sp.	22	12	8	42	0.61
	Elattoneura nigra Kimmins, 1938!	70	109	42	221	3.18
	Elattoneura sp.!	6	4	69	79	1.14
	Total number of species	17	16	20		
	Abundance	1576	1738	1209		

and agricultural habitat (est = 0.877 ± 0.482 , t = 1.818, p = 0.078) (For the full models, see Appendix 1 and 2).

Beta diversity

Mature forest and forest margin habitats had the greatest pairwise beta diversity with 43% dissimilarity between these habitat types. Agricultural habitat was much more similar to forest margin in terms of species composition: Ds = 18%. Conversely, the community composition of mature forest habitats was slightly more similar to agricultural habitats than it was to forest margin habitats (Ds = 35%).

Odonate community structure as an indicator of freshwater habitat quality

The CCA analysis demonstrated that canopy cover, depth and conductivity strongly correlated on both axes, while turbidity (% clarity) and surface water temperature correlated well on axis 1, but were poorly represented by axis 2 (Figure 4, Table 3). Turbidity was low in the mature forest, but high in the forest margin and agricultural habitats, where a higher number of the generalist and heliophilic species were found (e.g. P. lucia, P. portia, P. flavescens, N. pujoli and Ceriagrions). Surface water temperature was higher in the forest margins and agricultural habitats than the mature forest. Species such as Chlorocypha selysi, Micromacromia zygoptera, U. cincta, Phaon camerunensis and L. dissimulans responded to low surface water temperature along axis 1 in

Table 2. A complete list of the Anisopterans (dragonflies) in the three habitat classes within the study area. Species classified as forest specialist are represented by asterisk ($_*$), generalist species are represented by exclamation mark (!) and heliophilic species are represented by number sign (#). Identification of generalist, specialist and heliophilics were done following Dijkstra and Clausnitzer (2014) and African Dragonflies and Damselflies Online (http://addo.adu.org.za)

Family	Anisoptera species	Agricultural habitat	Mature forest	Forest margin	Total	Relative abundance
Aeshnidae	Gynacantha bullata Karsch, 1891*	0	1	0	1	0.01
Gomphidae	Onychogomphus sp.!	45	0	50	95	1.37
Libellulidae	Nesciothemis pujoli Pinhey, 1971#	36	0	27	63	0.91
	Chalcostephia flvifrons Kirby, 1889#	0	0	21	21	0.30
	Cyanothemis simpsoni Ris, 1915!	31	3	71	105	1.51
	Eleuthemis buettikoferi Ris, 1910!	98	1	0	99	1.43
	Hadrothemis coacta (Karsch, 1891)	3	0	0	3	0.04
	Micromacromia zygoptera (Ris, 1909)*	0	28	0	28	0.40
	Neodythemis klingi (Karsch, 1890)!	51	38	23	112	1.61
	Orthetrum abbotti Calvert, 1892!	2	0	3	5	0.07
	Orthetrum austeni (Kirby, 1900)#	11	0	19	30	0.43
	Orthetrum chrysostigma (Burmeister, 1839)!	23	0	12	35	0.50
	Orthetrum guineense Ris, 1909!	22	0	34	56	0.81
	Orthetrum icteromelas Ris, 1910#	4	0	3	7	0.10
	Orthetrum julia Kirby, 1900!	118	25	193	336	4.84
	Orthetrum microstigma Ris, 1911#	17	4	55	76	1.10
	Orthetrum monardi Schmidt, 1951	2	0	4	6	0.09
	Ortetrum sp.	0	0	9	9	0.13
	Orthetrum stemmale (Burmeister, 1839)#	33	4	32	69	0.99
	Orthetrum trinacria (Selys, 1841)#	5	0	0	5	0.07
	Palpopleura lucia (Drury, 1773)#	69	0	230	299	4.31
	Palpopleura portia (Drury,1773)#	36	0	195	231	3.33
	Pantala flavescens (Fabricius, 1798)#	33	0	153	186	2.68
	Tetrathemis camerunensis (Sjöstedt, 1900)#	0	3	0	3	0.04
	Trithemis aconita Lieftinck, 1969!	52	18	56	126	1.82
	Trithemis annulata (Palisot de Beauvois, 1805)!	0	0	12	12	0.17
	Trithemis arteriosa (Burmeister, 1839)!	131	0	183	314	4.71
	Trithemis dichroa Karsch, 1893!	19	0	37	56	0.81
	Trithemis imitata Pinhey, 1961!	0	0	13	13	0.19
	Trithemis kirbyi Selys, 1891!	0	0	16	16	0.23
	Total number of species	22	10	24		
	Abundance	841	125	1451		

the mature forest, where canopy cover was denser and positively correlated along both axes 1 and 2 (Figure 4, Table 3). Channel width and dissolved oxygen (DO) of the water bodies were positively correlated with each other along axis 1, where DO levels increased with the width of the rivers. Species like *O. julia*, *O. microstigma* and *O. stemmale* showed tolerance to wide variations on DO concentration levels as the width of the rivers expand further downstream. In contrast, conductivity and total dissolved solids (TDS) showed similar trend with negative correlation on axis 1, but positive correlation on axis 2 (Table 3).

In general, the mature forest habitats were characterized by lower water temperature, conductivity, dissolved solids, and shallower depth than the degraded habitats (agricultural and forest margin habitats) (Figure 4), while forest margin and agricultural habitats exhibited higher turbidity, less canopy cover, and lower DO levels than mature forest habitats (Figure 4). Accordingly, we have tentatively identified two potential indicator groups of odonate species for these environmental correlates of the alternative land use types. These potentially important indicator species are circled in Figure 4 and listed in Table 4.

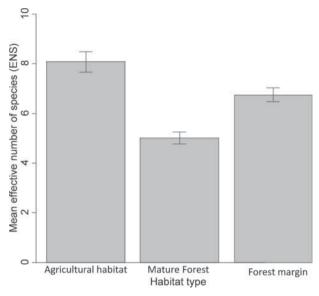


Figure 2. Mean effective number of species of odonates sampled in agricultural habitat, mature forest and forest margin habitat, across the three rivers. Error bars represent standard errors.

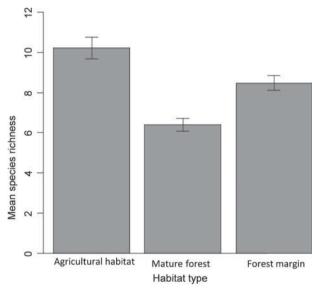


Figure 3. Mean species richness of odonates in the agricultural habitat, mature forest and forest margin habitats, across the three rivers. Error bars represent standard errors.

Discussion

Abundance and dominance of Odonata species

Among the species recorded, S. ciliata and C. luminosa were dominant in the Adensu, Densu and Supon rivers, which characteristically have fast flowing water and canopied riparian vegetation structure, and which are moderately degraded. These features are known to represent the preferred habitat type of these species (Dijkstra, 2007). Similarly to our findings, Acquah-Lamptey

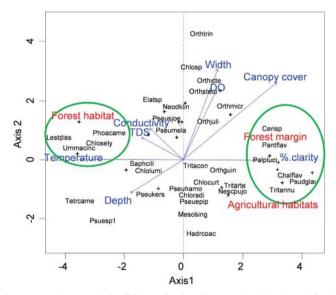


Figure 4. Canonical correspondence analysis (CCA) ordination diagram, showing the relationship between environmental variables and odonate species across the three river systems. Species names are abbreviated with the first four letters of the genus and the first four letters of the species (e.g. *Pantala flavescens: Pantflav*). The blue arrows represent each of the environmental variables plotted pointing in the direction of maximum change of explanatory variables across the three riverine systems. Species located within the green ovals represent potentially good candidates for local indicator species of freshwater ecosystem health (left side of graph) or degradation (right side of graph), respectively. The plus sign (+) represent Odonata species which were not shown in the ordination diagram (see Table 4 for a complete list of species located within the ovals).

Table 3. Summary of CCA eigenvectors showing the levels of correlation with the first two axes of the environmental variables of the three habitats. Asterisks ($_*$) indicate significance (< 0.05), following Monte Carlo permutation procedures.

Axis 1	Axis 2	R^2	<i>p</i> -value
0.99	- 0.01	0.04	0.050*
0.77	0.64	0.09	0.004**
0.36	0.94	0.05	0.014*
-0.86	-0.54	0.02	0.154
-0.73	0.69	0.01	0.400
-0.89	0.47	0.01	0.390
0.43	0.90	0.03	0.085
-0.99	0.01	0.06	0.010**
40.1	36.8		
76.9			
	0.99 0.77 0.36 - 0.86 - 0.73 - 0.89 0.43 - 0.99 40.1	0.99 - 0.01 0.77 0.64 0.36 0.94 - 0.86 - 0.54 - 0.73 0.69 - 0.89 0.47 0.43 0.90 - 0.99 0.01 40.1 36.8	0.99 - 0.01 0.04 0.77 0.64 0.09 0.36 0.94 0.05 - 0.86 - 0.54 0.02 - 0.73 0.69 0.01 - 0.89 0.47 0.01 0.43 0.90 0.03 - 0.99 0.01 0.06 40.1 36.8

et al. (2013) found *S. ciliata* to be the most dominant Zygoptera species along Densu River. The high occurrence of *P. melanicterum* along the rivers may be attributed to the widespread nature of this species, which can utilize a wide range of habitats, both open and shaded by gallery forest along streams and rivers (Dijkstra, 2017). *Mesocnemis singularis* was the fourth most abundant zygopteran species across the sites, and this species tended to be associated with the presence of rocks in the water bodies, which they utilize as a perching and emergence substrate (Dijkstra & Cluasnitzer, 2014). Therefore the high abundance of *M. singularis* may be linked to the rocky nature of rivers, especially along Densu River, although the presence of rocks was not one of our environmental predictor variables.

Table 4. List of Odonata species circled in Figure 4 (potential indicator species) in both the degraded (agricultural habitats and forest margin) and mature forest habitat.

Potential indicator Odonata species	Habitat type		
Ceriagrion glabrum			
Ceriagrion sp.	Agricultural habitats and forest margin		
Pseudagrion glaucoideum			
Pseudagrion sp2			
Chalcostephia flavifrons			
Palpopleura lucia			
Palpopleura portia			
Pantala flavescens			
Trithemis annulata			
Trithemis imitata			
Trithemis kirbyi			
Phaon camerunensis	Mature forest habitat		
Lestes dissimulans			
Gynacantha bullata			
Úmma cincta			
Chlorocypha selysi			
Micromacromia zygoptera			

The most dominant Anisoptera species across all sites was O. julia, and this species was widely distributed in all three rivers. Orthetrum julia is mostly found in forest habitats, but not exclusive to this habitat type (Dijkstra & Clausnitzer, 2014). The isolated patches of gallery forest along the agricultural habitat and forest margin are conducive habitat for these species, hence their high abundance in the entire study area. Trithemis arteriosa, a generalist and the second most abundant Anisoptera species, prefers open habitats (Dijkstra, 2017), which may be due to their thermoregulation requirements. This may explain why they were recorded only in the forest margin and agricultural habitats, which were characterized by open canopy cover. Heliophilic species like P. lucia, P. portia and the Ceriagrions were present in areas with stagnant water bodies (lagges). Their populations were largely restricted to the highly degraded forest margin at Densu, Supon and Adensu Rivers (due to small scale mining activities). These disturbances created pools which provided alternative habitats and resources for their survival. Gynacantha bullata was the only crepuscular species recorded in this study, and this was so because our sampling was conducted during the day.

Odonata community assemblages as indicator function among the habitats

The agricultural habitats had the highest estimated effective number of species (ENS) and species richness of odonates, likely because this habitat was characterized by patches of gallery forest interspersed with more disturbed areas of the river corridor. These patchy disturbances present diverse microhabitats for the colonization and utilization of generalist dragonfly and damselfly species. The generalists were able to utilize wide ranges of habitat, both temporary and permanent water bodies in the riparian corridors (Samways, 1989). This was reflected in the high number of generalist species encountered in the agricultural habitats, and these are also noted for their lower conservation value (Aratrakorn, Thunhikorn, & Donald, 2006; Waltert et al., 2004). The abundance of these generalists in the agricultural habitat may have accounted for the higher species richness there. Similarly, owing to thermoregulation and flight behavior of odonates, larger dragonflies belonging to the Aeshnidae and Libellulidae families are "fliers" in nature which outcompete "perchers" in open habitats (Corbet, 2005; Corbet & May, 2008).

The fliers require more open habitats to thermoregulate. The high abundance of species from the family of Libellulidae in the agricultural habitat was probably due to the preponderance of anthropogenic disturbances there, including small scale mining, illegal logging and farming, which created a more favourable thermal microhabitat for these tropical dragonflies. This finding agrees with other studies that found species richness of odonates to be higher in agricultural habitats. For example, Samways (1989) found farm dams to be suitable habitats for the conservation of dragonflies. Similarly, Ferreira-Peruquetti and Fonseca-Gessner (2003) and Hofhansl and Schneeweihs (2008) also reported higher number of species of odonates in cultivated areas as compared to pristine forest.

The moderate disturbance levels in the forest margin habitat may have contributed to its status as the second most abundant in odonate assemblages, through the creation of habitat heterogeneity via secondary forest growth and small scale mining regimes. Similarly, activities of small scale mining in the forest margin created mined pools, which were exploited by a high abundance of heliophilic species assemblages. This finding that species richness was relatively high in disturbed, forest margin sites, was consistent with other studies especially in the tropics (Clausnitzer, 2003) and subtropics (Samways & Steyler, 1996), where species richness was reported to be higher in the slightly disturbed habitats compared with pristine habitats. Samways and Grant (2008) also observed a positive impact of moderate disturbances on species diversity and richness of Odonata in open savannah streams and rivers.

The mature forest habitat was typically species poor, and was mostly dominated by damselflies which are characteristically perchers, especially the Calopterygidea (e.g. *U. cincta*, *C. selysi*), smaller Coenagrionids (e.g. *Pseudagrions*) and Protoneuridae (*E. nigra*), which utilized the forest structure as perching substrate. Furthermore, some damselflies oviposit endophytically and require vegetated oviposition substrates to carry out their reproduction. These reproductive requirements, in tandem with their lower thermoregulation requirements and their generally higher degree of habitat specialization, explain partly why most of the species encountered in the forest habitat were damselflies. Most dragonflies, on the other hand, required open habitat to thermoregulate and preferred to inhabit more disturbed areas. Thus there were relatively fewer numbers of anisopterans in the forest habitat. The dense canopy cover of the forest habitat provides a conducive environment to most forest specialist damselflies and dragonflies, which are relatively more species-poor and of higher conservation concern than heliophilic or generalist species. Similarly, Kinvig and Samways (2000) found lower but more specialized odonate species diversity from rivers under an intact primary forest canopy with only local sunspots in South Africa.

Most of the species encountered in the disturbed habitats were generalist and heliophilic dragonfly species, having wider dispersal ability and low conservation status. These species are good candidates as negative indicators of habitat quality as they colonize and increased in abundance as the habitat tends to be degraded. The influx of disturbance-tolerant species into a more open landscape, especially secondary habitats, has the potential to increase interspecific competition, which may lead to extinction of the stenotopic species in the ecosystems (Dijkstra & Clausnitzer, 2006; Oppel, 2006). In general, the mature forest habitat served as refuge to most unique and specialized odonates, while the disturbed habitats were mostly inhabited by eurytopic generalist and heliophilic species which have wide ranges (Clausnitzer, 2003). Clausnitzer et al., (2009) and Dolný, Harabiš, Bárta, Lhota, and Drozd (2012) concluded that disturbance may cause reductions in stenotopic and perching odonate species assemblages due to the loss of complex structure of the forest canopy, a conclusion that is further supported by our results. It can be further inferred from the findings in this study and other references (e.g. Van Biervliet, Wiśniewski, Daniels, & Vonesh, 2009) that deforestation does not only render habitats unsuitable for the colonization and reproduction for forest specialist species, but also of other equally threatened forest freshwater biota.

Beta diversity

Dissimilarity in species diversity between the mature forest and the forest margin habitats may result from differences in magnitude of disturbances between these two habitats. The forest margin habitats along the rivers were subjected to anthropogenic pressure, owing to small scale mining activities and isolated patches of gallery forest. Thus, forest specialist species such as M. zygoptera, T. cammerunensis, L. dissimulans and G. bullata were absent in the forest margin, while species of less conservation value such as the heliophilics (e.g. P. portia, P. lucia and C. glabrum), were dominant. This observation supports the hypothesis that fragmentation of natural habitats results in an altered species assemblage which tends to favour eurytopic generalist species, where they achieve dominance in the odonate community (Clausnitzer, 2003; Samways & Steytler, 1996; Stewart & Samways, 1998). The similarity in species representation between the agricultural and forest margin habitats can be linked to similar spatio-temporal scale in disturbances in each of these habitat types, such as small scale mining, open canopy cover and isolated patches of gallery forest. Disturbance gradients tend to shape the Odonata communities; hence, the observed similarity in the species composition between the agriculture habitats and the forest margin.

Conclusions

Dragonflies are widely used as indicators of the quality of freshwater habitats and the environment, because of their sensitivity to habitat alteration. Studies on odonate responses to ecosystem disturbance are scant in Ghana. Our study sought to determine the impacts of anthropogenic habitat disturbance on Odonata community structure. Our results demonstrate that odonate generalist and heliophilic species such as P. lucia, P. portia, T. arteriosa and Ceriagrions were more abundant in the agricultural habitats and the forest margins, where agriculture activities, mining and illegal timber logging created open canopy, increased water turbidity and lowered dissolved oxygen concentration. Alternatively, forest-specialist species such as M. zygoptera, U. cincta and C. selysi were prominent in the less disturbed mature forest habitat, characterized by lower temperatures, less turbidity, and denser canopy cover. The results suggest that observed changes in odonate communities linked to human-led disturbance could be used as monitoring tools for riverine ecosystem health in Ghana, and may be useful indicators to prioritize conservation intervention along the three rivers that drain through the Atewa Range Forest Reserve. The data also include novel records for many species of odonates in this part of the world, improving our understanding of global and local drivers of Odonata distributions and diversity.

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Supplemental data

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Appendix 1. Summary of the best model and the output for the effective number of species

Formula: Effective number of species \sim temperature + width + presence of lagges + canopy cover + habitat type + season + latitude + longitude + (1 | river/site/visit). Asterisks (*,*) indicate significance (< 0.05).

Fixed effects	Estimate	Std. Error	Df	t value	$Pr\left(>\left\vert t\right\vert \right)$
(Intercept)	288.743	116.965	36.880	2.469	0.018*
Temperature	0.441	0.210	55.600	2.096	0.041*
Width	0.282	0.120	31.690	2.347	0.025*
Present of lagges	0.882				
66	0.474	28.420	1.861	0.073	
Canopy cover	-0.035	0.009	47.510	-4.016	0.0002***
Forest versus agriculture	1.692	0.692	29.490	2.445	0.021*
Forest versus forest margin	0.816	0.606	30.180	1.346	0.188
Forest margin versus agriculture	0.877	0.482	32.630	1.818	0.078
Season (wet versus dry)	1.263	0.280	133.710	4.508	1.41e-05***
Latitude	-37.612	14.980	36.370	-2.511	0.017*
Longitude	70.820	40.016	35.390	1.770	0.085

Appendix 2. Summary of the best model and output for the species richness

Formula: Species richness ~ width + present of lagges + canopy cover + conductivity + turbidity + habitat type + latitude + longitude + season + $(1 \mid river/site/visit)$. Asterisks (*) indicate significance (< 0.05).

Fixed effects	Estimate	Std. Error	Df	t value	$\Pr\left(> t \right)$
(Intercept)	617.223	161.130	37.360	3.831	0.001***
Width	0.414	0.140	25.970	2.952	0.007**
Presence of lagges	1.038	0.523	22.110	1.987	0.059
Canopy cover	-0.038	0.009	33.180	-3.906	0.0004***
Conductivity	-9.174	11.178	41.960	-0.821	0.416
Turbidity	-0.018	0.004	45.060	-4.397	6.63e-05***
Forest versus agriculture	1.317	0.842	24.750	1.564	0.131
Forest versus forest margin	1.057	0.676	23.760	1.564	0.131
Forest margin versus agriculture	0.260	0.631	28.220	0.412	0.683
Latitude	-80.115	21.027	38.060	-3.810	0.0005***
Longitude	204.322	57.599	34.780	3.547	0.001**
Season (wet versus dry)	1.699	0.318	115.490	5.354	4.43e-07***